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Research Article

Prioritizing stream network connectivity for species conservation and sustainable planning

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Abstract

Ecological connectivity is crucial for amphibian conservation amid habitat fragmentation from human development. This study assessed stream network connectivity for two stream-breeding amphibians, *Rana sauteri* and *Odorrana swinhoana*, across an entire river catchment using the MaxEnt modeling framework. Multiscale stream order predictors represented stream network spatial structure across terrestrial habitats, while citizen-science occurrence and roadkill data serve as proxies for distribution and movement, enabling model construction and cross-validation without direct movement data. Most models performed significantly better than random expectations ($p < 0.05$–0.001), with high predictive power (AUC = 0.79–0.93; CBI = 0.74–0.97). Tree cover dominated predictor importance (41–70%), while stream order contributed substantially (17–23%) and showed strong predictive power, underscoring the importance of stream networks. *R. sauteri* responded at broader spatial scales across both occurrence and roadkill models (stream order 50–750 m; tree cover 150–2000 m), whereas *O. swinhoana* responded at intermediate scales (150–500 m; 250–1500 m), reflecting differences in habitat preferences and breeding behavior. In cross-dataset validation, occurrence models effectively predicted roadkill distributions (AUC = 0.88–0.92), while roadkill models transferred less successfully (AUC = 0.68–0.81), confirming their complementary ecological signals. These results demonstrate that stream order effectively captures the spatial hierarchy of amphibian connectivity across an entire catchment. Our framework enables connectivity analysis in data-limited contexts. The approach can be incorporated into Environmental Impact Assessments to support environmental planning and design by identifying scales of connectivity influence, altitudinal ranges, and topographic features such as valley-bottom zones where habitat suitability and roadkill risk overlap. Ultimately, this approach promotes stream network connectivity that sustains the movement and persistence of multiple taxa, contributing to biodiversity conservation and sustainable development.

Key words: Bioclimatic variables, riparian corridor, roadkill mitigation, shelterbelt planting, Strahler order, topographic indices, vegetation indices

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Introduction

Ecological connectivity enables wildlife to access resources, maintain gene flow, and adapt to environmental changes, although its influence on genetic diversity may differ among habitat types and is often stronger in highly connected systems such as aquatic networks (Fischer and Lindenmayer 2007; Rudnick et al. 2012). Yet, human development increasingly disrupts these pathways, fragmenting habitats and altering ecosystem functions, with effects on species abundance and richness that depend on habitat quality and landscape context and that can range from biodiversity loss to localized increases in some taxa (Fischer and Lindenmayer 2007; Haddad et al. 2015; Wilson et al. 2016; Scanes 2018; Tyagi et al. 2024). Maintaining connectivity has therefore become a cornerstone of biodiversity conservation (Taylor et al. 1993), shifting focus from isolated protected areas to integrated landscape-scale management (Fischer and Lindenmayer 2007; Haddad et al. 2015; Keeley et al. 2019; Albers et al. 2023b). Global initiatives such as the Kunming–Montreal Global Biodiversity Framework and the UNEP-WCMC Connectivity Conservation Focal Initiative emphasize the need to operationalize ecological connectivity and international biodiversity targets within policy, planning, and design at regional and local scales (WCMC n.d.).

Despite this recognition, effective implementation remains constrained by limited data on species movements. Connectivity models typically require dispersal information that is often lacking or difficult to obtain (Albers et al. 2023a). This limitation hinders the accurate identification of ecological corridors and barriers, creating uncertainty in conservation prioritization and landscape planning (Keeley et al. 2019; Liczner et al. 2024). To address this gap, researchers have developed methods to estimate connectivity without direct movement data, combining structural landscape metrics with empirical field observations (Laliberté and St-Laurent 2020; Paemelaere et al. 2023; Iverson et al. 2024). Conservation planning therefore increasingly depends on indirect indicators of movement and habitat connectivity, such as habitat suitability or roadkill risk (Liczner et al. 2024). Studies integrating species occurrence and roadkill data have proven particularly valuable, as occurrence points delineate habitat suitability, whereas roadkill locations act as proxies for movement and barriers (Cerqueira et al. 2021; Iverson et al. 2024). Although species distribution models have been widely applied to analyze species occurrence patterns or, separately, roadkill distributions (Cerqueira et al. 2021; Iverson et al. 2024), their combined use as complementary indicators of habitat suitability and movement-related risk remains uncommon in applied planning contexts (Laliberté and St-Laurent 2020; Paemelaere et al. 2023). Reliable inference from such proxies is essential to translate connectivity research into practical conservation tools (Laliberté and St-Laurent 2020; Paemelaere et al. 2023; Liczner et al. 2024). Embedding proxy-based connectivity analyses into the planning process can help prevent environmental degradation in advance and reduce costly retrofitting later (Torres et al. 2022; Paemelaere et al. 2023). Environmental Impact Assessments (EIAs) provide a practical framework for incorporating these analyses early in the planning process (Karlsson and Bodin 2022; Torres et al. 2022; Paemelaere et al. 2023), ensuring that connectivity assessments are data-driven and tailored to species, landscape context, and project goals (Kim et al. 2024; Liczner et al. 2024; Keeley et al. 2025). Therefore, integrating

occurrence and roadkill data can provide practical connectivity indicators for ecological landscape planning and design.

Species with limited mobility are disproportionately affected by connectivity loss (Hand et al. 2014). Amphibians exemplify this vulnerability because of their limited movement capabilities, dependence on both aquatic and terrestrial habitats throughout their life cycle, and the restricted habitat preferences of many species, which tend to limit dispersal and increase sensitivity to habitat loss (Arntzen et al. 2017; Churko et al. 2020). Their seasonal migratory and juvenile dispersal movements create complex connectivity needs that are difficult to capture without detailed tracking data, particularly where movements vary between life stages and landscape contexts (Semlitsch 2008; Pittman et al. 2014). Thus, amphibians serve as suitable focal species to evaluate connectivity within stream networks.

The importance of connectivity is further highlighted by Almpanidou et al. (2014), who found that connectivity, rather than habitat quality alone, drives bear movement patterns, with individuals using networks of both high- and low-quality patches instead of only high-quality ones. This example illustrates that focusing on habitat quality alone may overlook movement routes through less suitable areas, whereas integrating structural connectivity can reveal pathways missed by traditional habitat-suitability models, a principle that also applies to amphibians. Therefore, integrating spatial structure into species distribution models can help overcome this limitation by jointly identifying suitable habitats and connectivity elements (Dondina et al. 2018). Stream networks, serving as structural backbones of landscape connectivity, can help bridge this conceptual gap (Cheng et al. 2016; Kuemmerlen et al. 2019). For amphibians, incorporating stream order within species distribution models provides a means to integrate hydrological structure with habitat suitability inferred from occurrence records and with movement-related mortality risk inferred from roadkill records. Stream order was selected as a predictor because it integrates hydrological hierarchy, riparian structure, and potential movement pathways, making it particularly relevant for stream-breeding amphibians whose life cycles depend on both aquatic and terrestrial habitats. Moreover, incorporating stream order across multiple spatial scales of habitat context allows a more ecologically realistic assessment of amphibian connectivity (Gould and Peterman 2021). The resulting quantitative outputs describe continuous gradients of occurrence suitability and roadkill risk rather than fixed corridors, which better align with the random and dispersive nature of amphibian movements (Iverson et al. 2024). Such outputs can also be operationalized within EIA frameworks, providing standardized and comparable indicators of landscape permeability and impact zones (Kor et al. 2022; Paemelaere et al. 2023).

In this study, we assessed amphibian connectivity within stream networks using the MaxEnt species distribution modeling framework at the catchment scale. Stream order was used to represent the spatial structure of the stream network, and a multiscale moving-window approach was applied to encompass both aquatic and adjacent terrestrial habitats. In the absence of direct movement data (e.g., dispersal or migration), citizen science occurrence and roadkill records were used as complementary proxies for amphibian movements, enabling model construction and cross-dataset validation to examine whether spatial patterns inferred from one ecological signal—either habitat occurrence or road mortality—are reflected in the other. By comparing predictions across occurrence and roadkill datasets, this validation provides insight into the trans-

ferability of inferred connectivity patterns. We aimed to evaluate whether multiscale stream-order predictors effectively describe amphibian occurrence and roadkill distributions and whether these datasets reveal consistent stream-network connectivity patterns by jointly capturing occurrence-based suitability and movement-related mortality at aquatic–terrestrial interfaces. We therefore hypothesized that stream order, particularly when evaluated across multiple spatial scales, is associated with both amphibian occurrence and roadkill distributions, reflecting underlying stream-network connectivity patterns. We further sought to identify the key environmental predictors shaping occurrence and roadkill distributions of the focal species and to interpret these patterns in relation to species traits, providing insights into habitat preferences and behavioral responses to bioclimatic and topographic drivers. Finally, we aimed to derive landscape planning and design guidelines for incorporating stream network connectivity conservation into EIAs, thereby supporting sustainable development.

Materials and methods

Study area

The study area was conducted in the Danshui River catchment, located in northern Taiwan between 24.6°N and 25.3°N latitude and 121.3°E and 121.8°E longitude, covering an area of 2712 km^2 and elevations ranging from 0.5 m to 3421 m (Fig. 1). Land cover within the basin comprised 86% tree cover, 10.6% built-up area, 1.6% permanent water bodies, 0.9% grassland, and 0.5% cropland, calculated in this study from the ESA WorldCover land cover map (Zanaga et al. 2022). The average annual rainfall is 2275 mm, with a distinct wet season from May to October and a dry season from November to April. Mean monthly temperature ranges from 16.1 °C in January to 29.6 °C in July (Chen et al. 2019).

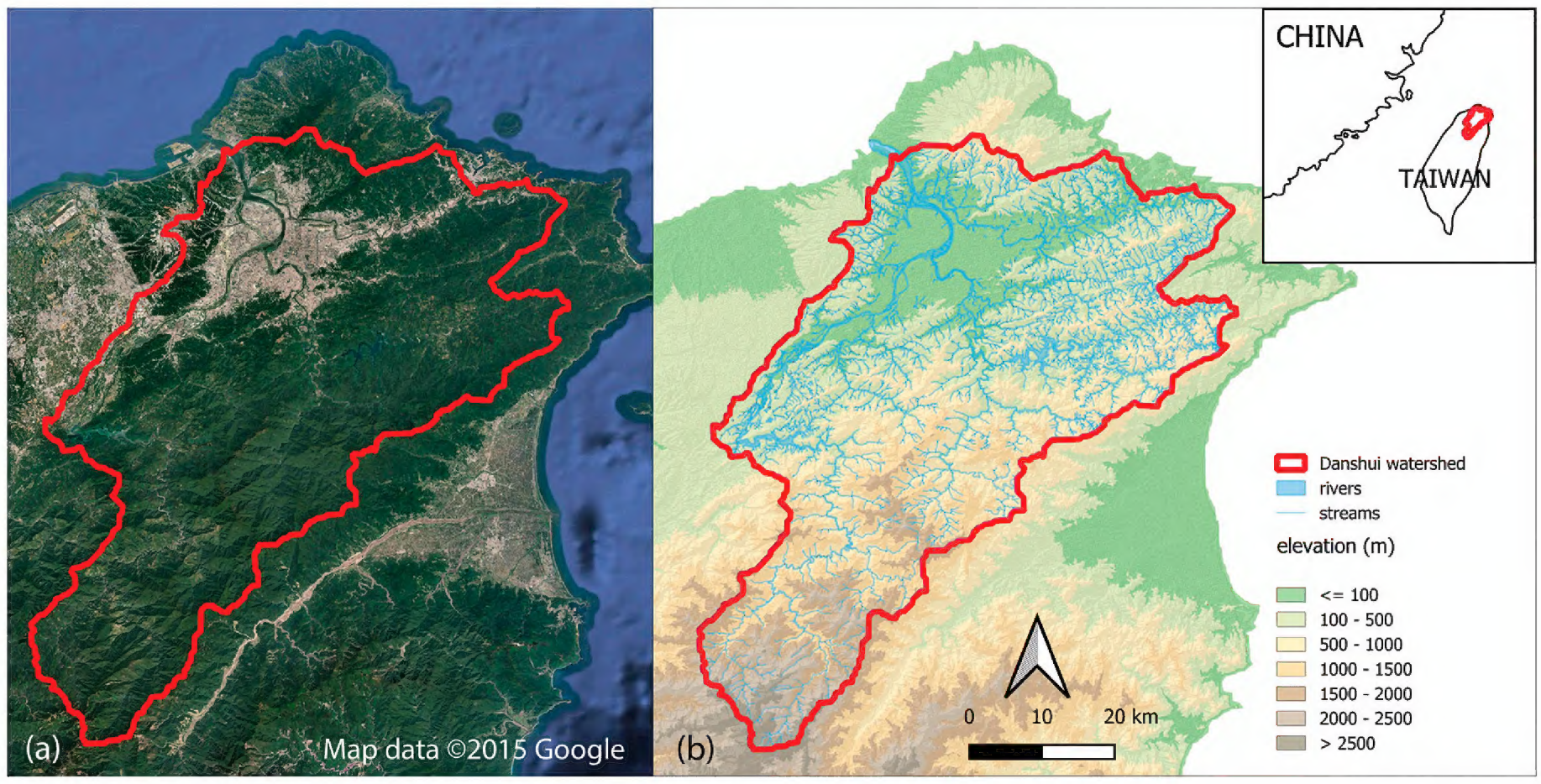

Figure 1. Danshui River catchment. **a.** Satellite image showing the urbanized and forested areas within the catchment; **b.** Elevation map overlaid with the river network. Human development is concentrated in the lower-elevation regions and extends along river valleys.

Streams within the catchment are generally short and steep because of the mountainous geomorphology. Although the catchment covers 7.5% of Taiwan's total area, it hosts 26% of the national population, concentrated in the Taipei metropolitan area (Yu et al. 2014). Residential, industrial, and agricultural developments are spread mainly along riparian corridors, and development pressure surrounding the Taipei metropolitan area is high (Lin et al. 2008; Huang et al. 2012). This catchment represents a gradient of urbanization and forest cover, providing an ideal setting to evaluate amphibian connectivity across heterogeneous landscapes.

Focal species

Rana sauteri and *Odorrana swinhoana* were selected as focal species because they represent divergent ecological strategies related to stream dependency. *R. sauteri* is classified as Vulnerable (VU) on the IUCN Red List, with habitat loss and roadkill identified as major threats (IUCN 2020b). Both species are stream-breeding amphibians inhabiting forested environments (IUCN 2020b, 2020a). *R. sauteri* is mainly active during the breeding season, when adults aggregate and migrate from forest to breeding streams (Lai et al. 2003). This makes it a well-known roadkill victim, and volunteer rescue missions for this species are organized across Taiwan on a regular basis (Frog in Sanshia n.d.; The Society of Wilderness n.d.). In contrast, *O. swinhoana* lives in or around streams throughout the year, exhibiting homing ability and sedentary behavior (Kam and Chen 2000; IUCN 2020a). Juveniles and subadults are active in nearby terrestrial habitats (Kam et al. 1998), such as in the litter layer near forest creeks (Huang and Hou 2004).

Occurrence records were obtained from the Taiwan Amphibians Database (TAD) (Yang et al. 2022) and roadkill records from the Taiwan Roadkill Observation Network (TaiRON) Dataset (Lin 2022), both accessed via the Global Biodiversity Information Facility (GBIF). These citizen-science projects are supported and monitored by researchers. The TAD has conducted systematic, large-scale surveys since 2007, providing data for amphibian distributions, Important Frog Area identification, and other key conservation indicators (Yang 2021), while the TaiRON has contributed substantially to roadkill mitigation research and applications in Taiwan (Hsu et al. 2018; Chyn et al. 2019; Zhao et al. 2023).

For *R. sauteri*, occurrence records were available for 2006, 2007, and 2012–2021, and roadkill records for 2012 and 2014–2017. For *O. swinhoana*, occurrence records covered 2006–2021, and roadkill records 2013–2017. We kept only the records within our study catchment (Fig. 2). Records without complete species identification and location coordinates were removed. Duplicate records in the same grid cell were also removed. The final datasets included (1) *R. sauteri* occurrence, n = 88; (2) *R. sauteri* roadkill, n = 11; (3) *O. swinhoana* occurrence, n = 437; (4) *O. swinhoana* roadkill, n = 31. Movement knowledge, including dispersal and migration patterns, remains limited for both species, with particularly scarce information on *R. sauteri* attributable to its cryptic behavior outside of breeding periods. This challenge is evident in citizen-science datasets, where the sample size for *R. sauteri* is markedly smaller than that for *O. swinhoana*, underscoring the inherent difficulties associated with studying elusive, forest-dwelling amphibians.

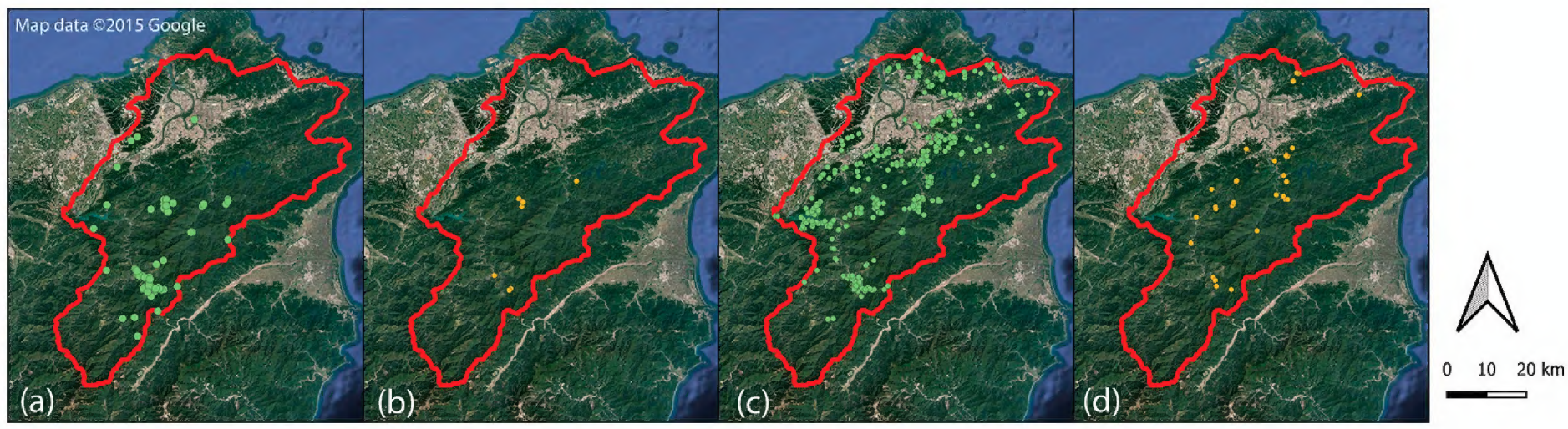

Figure 2. Occurrence and roadkill records of *R. sauteri* and *O. swinhoana* within the study watershed. **a.** *R. sauteri* occurrence records; **b.** *R. sauteri* roadkill records; **c.** *O. swinhoana* occurrence records; **d.** *O. swinhoana* roadkill records.

Environmental predictors

Multiscale predictors

Stream order, delineated using the Strahler method, was used to represent stream network characteristics in the study catchment. The Strahler system represents surface water flow patterns, including both permanent and temporary stream channels. This inclusive approach captures the full organization of the drainage network, regardless of whether water flow is continuous or seasonal (Strahler 1957). To quantify the influence of stream networks across the catchment, we employed moving-window calculations on the delineated stream orders. Based on exploratory analyses, multiscale buffers with radii of 50, 150, 250, 500, 750, 1000, 1250, 1500, and 2000 m were used, producing predictors ranging from streamorderR50 to streamorderR2000 (see Suppl. material 1: table S1 for descriptions). Stream order calculated with different moving-window radii demonstrated distinct spatial patterns reflecting the influence of streams within different distances throughout the entire catchment area. These spatial patterns were subsequently employed to assess and infer the corresponding movement patterns associated with amphibian dispersal or migration in this study.

Stream order was derived from 30 m resolution AW3D30 Digital Elevation Models (DEMs) (Japan Aerospace Exploration Agency 2021) using SAGA GIS 9.2.0 (Conrad et al. 2015). The AW3D30 is an open-access dataset and has been demonstrated to be suitable for stream and catchment delineation in mountainous terrains (Moges et al. 2023; Chymyrov 2021). In areas where streams were absent or obscured by built-up surfaces, we assigned Strahler order values of zero to locations with >75% built-up coverage, calculated from the ESA WorldCover land cover map (Zanaga et al. 2022). All moving-window analyses were conducted using the terra package (Hijmans 2023) in R 4.3.2.

Tree cover was included as a structural predictor, given its known influence on amphibian distribution (Matos et al. 2012; Campbell et al. 2024). We computed tree cover percentages (%) using the same multiscale moving-window buffers applied to stream order, resulting in predictors treecoverR50 to treecoverR2000. Employing multiple scales is essential for evaluating the relative importance of structural predictors (e.g., tree cover) versus spatial configuration (e.g., stream order), as the explanatory power of these predictors often shifts depending on the spatial extent of analysis (Kimberley et al. 2021; Liu et al. 2024). This

approach allows for the identification of the specific scale of effect at which these features influence distribution, thereby reducing the risk of overestimating a predictor's influence due to arbitrary scale selection (Laliberté and St-Laurent 2020; Liu et al. 2024). Tree cover at 10 m resolution was obtained from the ESA WorldCover dataset and aggregated to 30 m grids in R 4.3.2 (R Core Team 2023).

Local-scale predictors

In addition to spatial predictors, we also included bioclimatic, vegetation, and topographic variables (Suppl. material 1: table S1). Bioclimatic temperature and precipitation variables were derived from gridded historical daily data (0.05° resolution) based on local weather-station records collected from 2011 to 2020 (TCCIP 2024). The data were downscaled to a 30 m resolution using the clim.regression V2.0 provided by the same TCCIP platform, which applies bilinear interpolation and dynamic elevation adjustments (Lin et al. 2018, 2020; Lin and Chen 2023). From the downscaled climate data, we generated 19 bioclimatic variables using the biovars function in the dismo package (Hijmans et al. 2023) in R 4.3.2.

We also included three vegetation indices: Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), and Normalized Difference Red Edge Index (NDRE). NDVI is widely used in amphibian distribution studies to represent vegetation greenness (Arntzen 2006; Goudarzi et al. 2021). EVI has been found to effectively capture biomass variation and amphibian richness (Qian et al. 2007). NDRE was included for its ability to distinguish vegetation types in forested areas (Wavrek et al. 2023), which is the dominant land cover in our catchment. To account for seasonal variability when computing the indices, we selected remote-sensing images with low cloud cover from 15 January 2021, 12 March 2019, and 2 November 2021 (Silveira et al. 2007). The computations were performed using Harmonized Landsat Sentinel-2 (HLS) images (Masek et al. 2021) in QGIS (QGIS 2023).

Finally, we included 10 topographic predictors selected for their relevance to stream-network structure and previous amphibian studies. Slope, Heat Load Index (HLI), Topographic Position Index (TPI), Terrain Ruggedness Index (TRI), and Topographic Wetness Index (TWI) have been widely applied in amphibian distribution modeling (Groff et al. 2017; Riley et al. 2017; Goudarzi et al. 2021; Trumbo et al. 2023). Flow Accumulation (Flowacc) and Stream Power Index (SPI) were also included due to their relevance to stream networks and surface-water flows (Schmidt et al. 2011; Holenstein et al. 2022). In addition, we included the Wind Exposition Index (WEI), Hill Index, and Valley Index, following Huang and Hou (2004), who reported a lower abundance of anurans in litter layers at wind-exposed sites. All topographic predictors were calculated using AW3D30 DEMs in SAGA GIS 9.2.0 (see Suppl. material 1: table S1 for methods and parameters), except for HLI, which was computed using the spatialEco package (Evans and Murphy 2021) in R 4.3.2.

MaxEnt modeling framework

Modeling with limited sample sizes poses a significant risk of overfitting, wherein the model captures noise instead of the underlying biological signal. To address this challenge associated with small sample sizes in this study (*R. sauteri*

roadkill sample size n = 11), we employed the MaxEnt modeling framework. MaxEnt mitigates overfitting through the application of regularization, which imposes a penalty on model complexity, and by constraining the selection of feature classes (Merow et al. 2013). It has demonstrated strong predictive performance across small to moderate presence datasets, including 10–100 presence points (Wisz et al. 2008). MaxEnt was also selected for its capability to manage complex variable relationships (Merow et al. 2013; Perkins-Taylor and Frey 2020). A fine-scale modeling resolution of a 30 × 30 m grid was chosen for this study based on the literature regarding adult *O. swinhoana* movement (Kam and Chen 2000). *O. swinhoana* exhibits strong site fidelity, with a mean maximum movement distance of 15.4 ± 30.0 m and individual movements ranging from 0 to 179 m during the 24-month study period. This 30 × 30 m grid also allows for the analysis of the immediate context of a location, in contrast to the broader landscape context (Jones et al. 2024).

To mitigate the effects of sampling bias, we generated 10,000 target-group background points derived from the collective amphibian records, excluding the focal species, within each database (TAD and TaiRON Dataset), following the protocols of Barber et al. (2022). This target-group approach strengthens model robustness by utilizing the occurrences of taxonomically similar species as a proxy for sampling effort. By aligning the background data with the spatial distribution of sampling intensity, this method ensures that the model discriminates true environmental associations from artifacts of accessibility, preventing the prediction of distributions that merely reflect survey effort rather than habitat suitability.

All predictors were standardized using z-score transformation to ensure comparable scales for model evaluation. Initially, we constructed default MaxEnt models for each predictor category (e.g., stream order, tree cover, bioclimatic temperature) and removed predictors with permutation importance < 1%. We then calculated pairwise Spearman's rank correlations, removing the predictor with lower permutation importance from pairs where $|r| > 0.80$, a standard threshold for minimizing multicollinearity in species-distribution models (Sillero et al. 2021). Next, we constructed default models for each species, separately for the multiscale and local-scale predictors and for both occurrence and roadkill datasets, to account for potential interactions between categories. We again removed predictors with low permutation importance. Due to the different permutation importance levels exhibited by occurrence and roadkill models, predictors with permutation importance < 5% were removed from occurrence models and those < 1% from roadkill models. Remaining multiscale and local-scale predictors were then combined and evaluated for multicollinearity using Variance Inflation Factors (VIFs), excluding those with VIF > 10 (Heigl et al. 2017).

We then combined the remaining predictors (multiscale and local scale) to construct the final occurrence and roadkill models for both species. Because complex models may overfit and distort variable importance (Warren and Seifert 2011; Radosavljevic and Anderson 2014), we refined predictors further through model-parameter tuning and removed predictors with low permutation importance again. We tested (a) 25 parameter combinations of feature classes: 'L' (Linear), 'LQ' (Linear + Quadratic), 'LQH' (Linear + Quadratic + Hinge), 'LQHP' (Linear + Quadratic + Hinge + Product), and 'LQHPT' (Linear + Quadratic + Hinge + Product + Threshold); and (b) regularization multipliers from 1 to 5 (Morales

et al. 2017). All combinations were trained using three-fold cross-validation, and the model with the lowest corrected Akaike Information Criterion (AICc) was selected (Morales et al. 2017; Bao et al. 2022). We evaluated model performance with Area Under the Curve (AUC) and iteratively removed the predictor with the lowest permutation importance until the absolute difference between training and validation AUC (|AUC.diff|)—during cross-validation—reached its minimum. The model with the minimum |AUC.diff| was selected as the final model, representing a lower degree of overfitting and better generalization (Radosavljevic and Anderson 2014). MaxEnt model tuning and null-model tests were performed using the ENMeval 2.0 package (Kass et al. 2021) in R 4.3.2.

We then applied cross-dataset validation, in which occurrence models were evaluated against roadkill data and vice versa, to determine whether these datasets reflect convergent or distinct connectivity patterns associated with potentially different movement scenarios. This comparative analysis is essential, as prior research has demonstrated that both data types provide unique, complementary insights that together give a more complete picture of connectivity than either alone (Iverson et al. 2024). For a holistic model evaluation that avoids overemphasizing AUC's discriminative power alone (Hond et al. 2022; White et al. 2023), we complemented AUC evaluation using the Continuous Boyce Index (CBI) to assess model calibration (Hirzel et al. 2006). To evaluate the reliability of AUC and CBI scores, we conducted 100 null-model iterations following Bohl et al. (2019), a widely used approach that provides statistical support for the selected model and predictors in ecological niche modeling (Wheatcroft 2020; Sillero et al. 2023). The selected predictors were evaluated with relative importance quantified using MaxEnt permutation importance (PI), calculated as the normalized percentage decrease in training AUC resulting from random permutations of predictor values (Phillips et al. 2017). PI depends strictly on the final model and provides a standardized measure of the model's total dependence on each predictor. The relationships between predictor values and estimated suitability were evaluated using single-variable response curves, which isolate the species' response to a specific variable by creating a model using that variable alone (Phillips et al. 2017).

Finally, predicted habitat-suitability maps were projected onto the 3D shaded digital elevation model (DEM) of the study catchment, overlaid with the stream network. The outputs were visualized in both continuous (gradient) and binary formats. Binary maps were produced using the threshold that maximizes the sum of sensitivity and specificity, a method recommended for presence-only models (Liu et al. 2016). These visualizations were used to compare and interpret spatial patterns of predicted suitability for both occurrence and roadkill models.

Results

Key predictors

Predictor importance was evaluated and compared using their relative weights (PI values) within each model, allowing for a standardized comparison of their influences across models. Spatial predictors, stream order and tree cover, were consistently selected across multiple scales (Table 1) and displayed positive relationships with predicted suitability (Suppl. material 1: fig. S1) for occur-

Table 1. Key predictors retained in final models, with permutation importance (PI, %) values.

Predictors	Permutation importance (PI, %)			
	Rana sauteri		*Odorrana swinhoana*	
	occurrence model	roadkill model	occurrence model	roadkill model
Multiscale Spatial Predictors				
Stream Order				
streamorderR50m		8.0		
streamorderR150m			8.7	3.6
streamorderR500m	10.7			13.7
streamorderR750m		15.0		
Sum	**10.7**	**23.0**	**8.7**	**17.3**
Tree Cover				
treecoverR150m	31.6			
treecoverR250m			55.5	
treecoverR1500m				40.6
treecoverR2000m	37.8	69.5		
Sum	**69.4**	**69.5**	**55.5**	**40.6**
Local-scale Environmental Predictors				
Bioclimatic Temperature				
BIO1			4.4	
BIO8				23.6
Sum			**4.4**	**23.6**
Bioclimatic Precipitation				
BIO14	11.1			
BIO16			8.5	13.8
BIO18		7.5		
Sum	**11.1**	**7.5**	**8.5**	**13.8**
Vegetation				
NDRE_March	8.8		17.0	
Topography				
WEI			5.9	4.7

rence and roadkill models of both species. While tree cover was the most influential predictor overall, the significance of the stream network was revealed through the relative shift in importance between occurrence and roadkill models. Stream order was found to be markedly more influential in roadkill models (PI = 23.0%, *R. sauteri*; 17.3%, *O. swinhoana*) than in occurrence models (PI = 10.7%, *R. sauteri*; 8.7%, *O. Swinhoana*) for both species. This higher relative dependence indicates that while the stream hierarchy is a meaningful predictor of habitat suitability, it plays a comparatively stronger role in shaping the spatial movement patterns associated with road mortality.

For *R. sauteri*, the occurrence model selected a 500 m stream order radius, while the roadkill model included both 50 m and 750 m radii, suggesting bidirectional roadkill-related movements both toward and away from streams during breeding migrations, in contrast to the single pattern associated with the occurrence model. For *O. swinhoana*, the selection of the 150 m scale in both models

suggests overlap in inferred movement ranges between occurrence and roadkill models. However, the additional selection of the 500 m radius in the roadkill model, which is also characterized by a higher PI value, indicates that extended dispersal further beyond riparian zones is associated with increased roadkill risk.

Across all models for both focal species, tree cover was a persistent spatial predictor retained over a broad multiscale range from 150 m to 2000 m. It consistently dominated over other predictors, with PI values ranging from 40.6% to 69.5%, underscoring its significant role in determining amphibian distribution in the catchment. However, despite its high PI values, response curves indicated that its effect on predicted suitability was comparatively weaker than the positive relationship exhibited by stream order predictors (Suppl. material 1: fig. S2).

Bioclimatic predictors contributed varying relative importance (PI = 4.4–23.6%) across models. *R. sauteri* models selected only precipitation variables, with occurrence influenced by precipitation of the driest month (BIO14) and roadkill by precipitation of the warmest quarter (BIO18). *O. swinhoana* models selected both temperature and precipitation variables: annual mean temperature (BIO1) for occurrence, mean temperature of the wettest quarter (BIO8) for roadkill, and precipitation of the wettest quarter (BIO16) for both models. Moreover, BIO8 was the most influential bioclimatic predictor (PI = 23.6%), followed by BIO16 (PI = 13.8%), both in the roadkill model. This indicates that while occurrence distributions are shaped by general temperature conditions, roadkill patterns are jointly influenced by temperature and precipitation, with temperature emerging as the dominant factor.

Vegetation (NDRE–March) was selected in occurrence models of both species, emphasizing the importance of early-spring vegetation dynamics as a critical habitat parameter. Finally, wind shelter (WEI) emerged as an important predictor for *O. swinhoana*, with occurrence models showing slightly stronger sensitivity to wind exposure (PI = 5.9%) than roadkill models (PI = 4.7%), while both displayed negative responses to increasing exposure (Suppl. material 1: fig. S3).

Occurrence and roadkill suitability patterns

For both species, occurrence suitability extended more broadly and to higher altitudes than roadkill suitability, which was largely concentrated at middle elevations (Figs 3, 4). Predicted suitabilities closely followed the stream network, with suitable areas clustering along stream corridors and radiating into adjacent terrestrial sites, most notably in the roadkill models.

Within species, the *R. sauteri* occurrence model showed broader overall suitability, with the highest values concentrated at higher altitudes (Fig. 3). For *O. swinhoana*, both occurrence and roadkill suitability covered wider areas overall (Fig. 4) compared to *R. sauteri*. Binary maps highlighted these differences, with *R. sauteri* exhibiting patchier coverage, whereas *O. swinhoana* showed a more continuous pattern, with distributions concentrated along recessed valleys.

Model evaluation and validation

Model performance metrics are summarized in Table 2, and model settings are provided in Suppl. material 1: table S2. Models showed consistently strong predictive performance, with AUC ranging from 0.794–0.933 and CBI from 0.742–0.968.

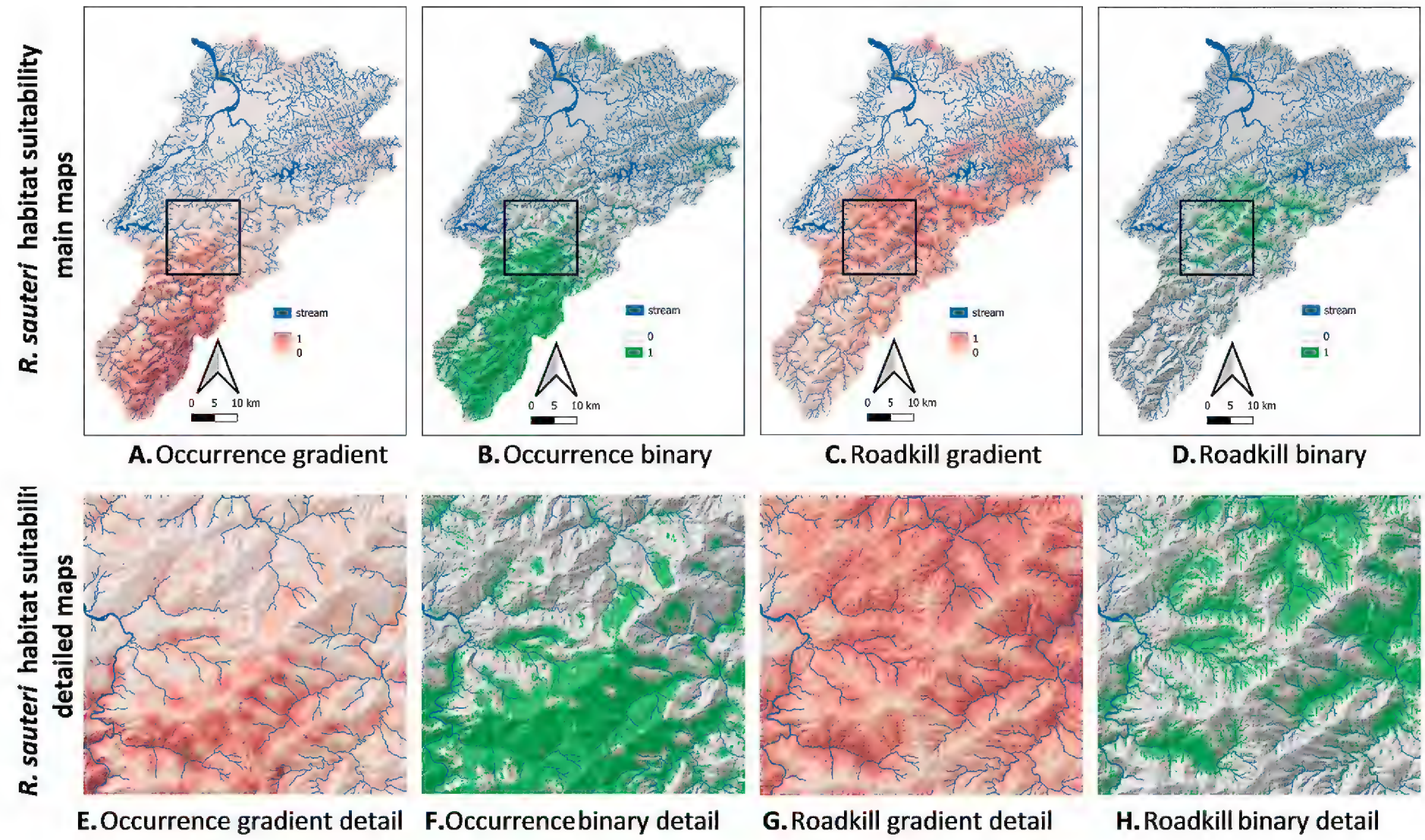

Figure 3. Habitat suitability of *Rana sauteri* overlaid with stream network. Panels **A–D.** show occurrence and roadkill suitability (gradient and binary outputs), while **E–H.** show detailed views of representative areas of the study landscape structure. Gradient maps are shown in red (darker = higher suitability) and binary maps in green (suitable areas).

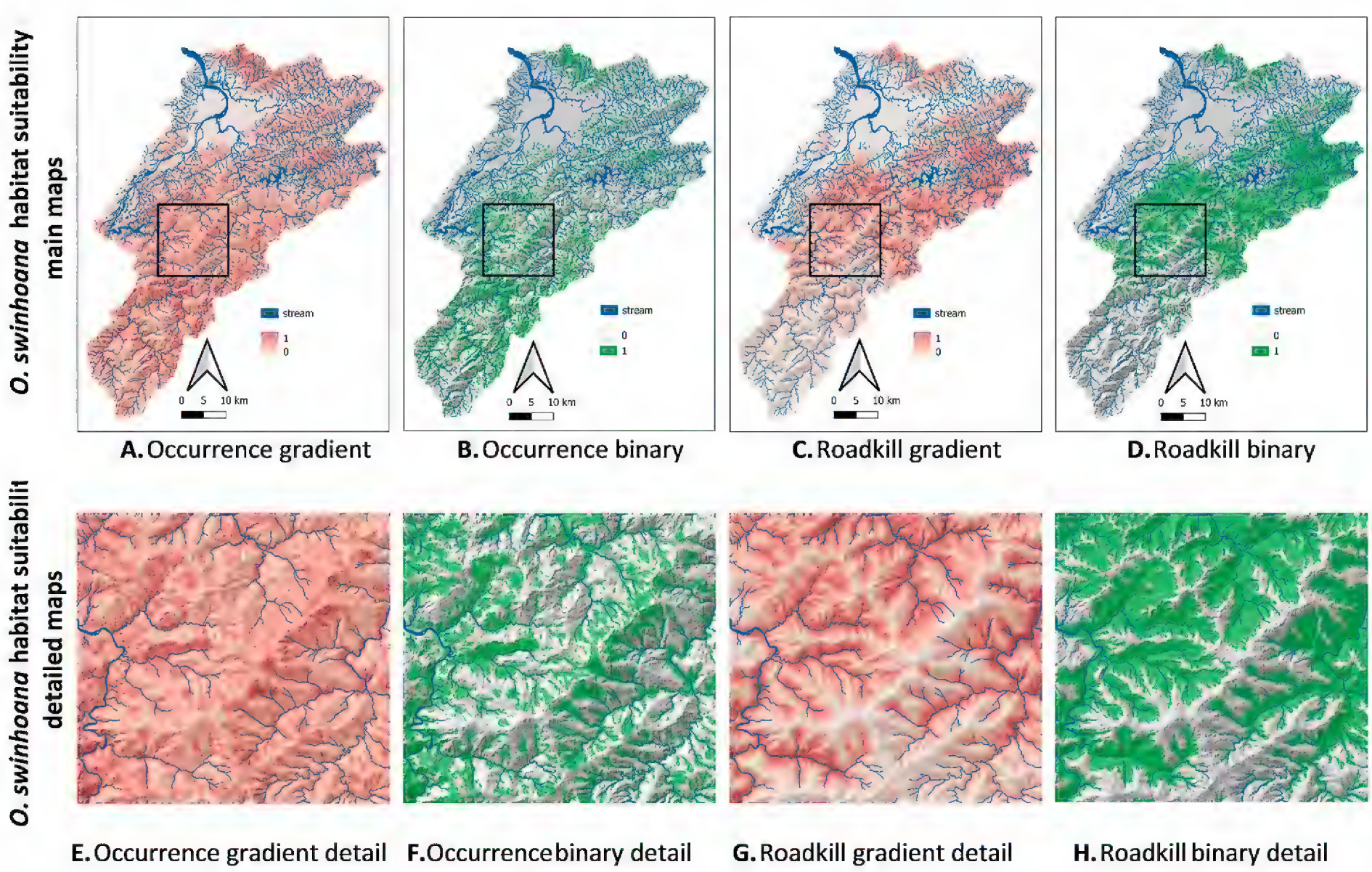

Figure 4. Habitat suitability of *Odorrana swinhoana* overlaid with stream network. Panels **A–D.** show occurrence and roadkill suitability (gradient and binary outputs), while **E–H.** show detailed views of representative areas of the study landscape structure. Gradient maps are shown in red (darker = higher suitability) and binary maps in green (suitable areas).

Table 2. Performance of Maxent models for *Rana sauteri* and *Odorrana swinhoana* based on cross-validation and cross-dataset evaluation. Metrics include AUC and CBI. Model settings are provided in Suppl. material 1: table S2.

Evaluation metric	*Rana sauteri*		*Odorrana swinhoana*	
	occurrence model	roadkill model	occurrence model	roadkill model
model training cross validation				
AUC.val (avg)	0.933***	0.893***	0.794***	0.832***
|AUC.diff|(avg)	0.018***	0.057**	0.024**	0.028***
CBI.val (avg)	0.828***	0.742***	0.968**	0.763***
model evaluation with cross-dataset				
AUC	0.918**	0.810**	0.884**	0.679**
CBI	0.877*	0.902	0.957	0.909

* p < 0.1, ** p < 0.05, *** p< 0.001, null model test p-values significance levels.
AUC.val (avg): average of the AUC calculated on the validation datasets.
|AUC.diff|(avg): average of the absolute values of the difference between train and validation dataset during cross validations.
CBI.val (avg): average Continuous Boyce Index calculated on the validation datasets.

Overfitting was limited, as indicated by low |AUC.diff| values (0.018–0.057). Occurrence models for both species performed strongly on their own data and also validated successfully with roadkill records (AUC = 0.884–0.918; CBI = 0.877–0.957), demonstrating that general habitat suitability patterns aligned with mortality locations. Roadkill models also performed well on their own data (AUC = 0.832–0.893; CBI = 0.742–0.763), but predictive ability was weaker when evaluated against occurrence records (AUC = 0.679–0.810). However, high CBI values (0.902–0.909) indicated good calibration despite lower discrimination, suggesting that predicted probabilities still reflected occurrence frequencies.

Null-model tests confirmed that the |AUC.diff| values were significantly lower than random expectations, while AUC and CBI metrics were significantly higher. For cross-dataset validation, all AUC metrics exceeded null distributions, whereas the CBI metric reached significance only for the *R. sauteri* occurrence model validated with roadkill data (Table 2; Suppl. material 1: figs S4, S5).

Discussion

This study demonstrates that stream networks, quantified using multiscale stream order predictors, and tree cover jointly shape amphibian distributions in human-transformed landscapes. By integrating occurrence and roadkill datasets across multiple scales, we captured habitat associations (occurrence models) alongside movement-related mortality risks (roadkill models), identifying sections of the connectivity network where movement coincides with elevated mortality and yielding complementary insights into connectivity processes. This joint analysis provides insights into species-specific functional connectivity by linking multiple movement scales associated with long-distance dispersal and road-crossing mortality, translating these patterns into actionable planning and design guidance for sustainable development. Such integration of occurrence- and roadkill-based predictors remains rare in SDM-based connectivity assessments (Paemelaere et al. 2023; Iverson et al. 2024). More broadly, our findings highlight how amphibians respond to key landscape

and environmental drivers, including hydrological, climatic, and vegetation factors, thereby advancing ecological understanding and offering practical guidance for biodiversity conservation, environmental planning, and design.

Key predictors

Stream order was more strongly associated with roadkill models (PI = 17.3–23.0) than with occurrence models (PI = 8.7–10.7), underscoring the importance of streams as movement corridors that can become zones of elevated mortality risk when intersected by roads. This pattern is consistent with amphibian movement ecology, as individuals frequently move along stream corridors during breeding and dispersal, increasing exposure to road crossings where roads intersect riparian networks (Semlitsch 2008; Pittman et al. 2014; Arntzen et al. 2017; Churko et al. 2020). While tree cover consistently dominated models across species (PI = 40.6–69.5%), stream order provided stronger predictive power (Suppl. material 1: figs S1, S2). This likely reflects amphibian reliance on forested habitats for food, shelter, and dispersal (Kam et al. 1998; Kam and Chen 2000; Huang et al. 2004), but suggests that stream networks may be more influential than broader habitat factors in shaping amphibian distribution and roadkill risk. Spatial scales differed by species. *R. sauteri* responded at broader scales across both occurrence and roadkill models (stream order 50–750 m; tree cover 150–2000 m), while *O. swinhoana* responded at intermediate scales (stream order 150–500 m; tree cover 250–1500 m). These differences should be interpreted with some caution, as discrepancies in the number of occurrence and roadkill records between species may influence model sensitivity and the detection of scale-dependent responses. Nonetheless, the observed patterns are consistent with species-specific habitat preferences and breeding behavior. *R. sauteri* inhabits hill forests and breeds in associated streams, followed by post-breeding terrestrial dispersal, as documented by IUCN (2020b), a pattern that likely reflects bidirectional movements: broad habitat associations with tree cover (150–2000 m occurrence) and localized dispersal risks along streams (50–750 m roadkill). *O. swinhoana* is also a stream-breeding species inhabiting hillside streams in broadleaf forests, with sedentary ecology and homing ability. Its reliance on local riparian zones suggests that individuals breed within their home range. By inhabiting riparian zones, it likely obtains sufficient environmental conditions and does not require long-distance movements (Kam and Chen 2000; IUCN 2020a). For *O. swinhoana*, the 150-m overlap across models underscores the importance of immediate riparian zones for both habitat suitability and roadkill risk. The additional 500 m association in roadkill models suggests that occasional dispersal beyond core habitats may increase exposure to roads, explaining the relatively higher importance of this scale (PI = 13.7) despite the species' sedentary ecology.

These multiscale associations directly inform functional connectivity, defined as the degree to which the landscape enables actual movement of individuals between habitat patches (Rudnick et al. 2012, Torres et al. 2022, and Liu et al. 2024). For stream-breeding and forest-dwelling amphibians such as *R. sauteri* and *O. swinhoana*, functional connectivity likely depends on low-resistance pathways provided by riparian corridors and forested cover, which facilitate both routine movements (e.g., to breeding streams) and occasional longer-distance

dispersal. The broader scales identified for *R. sauteri* (stream order up to 750 m, tree cover to 2000 m) suggest that larger connected areas are required to accommodate post-breeding terrestrial dispersal and occasional longer-distance movements that support metapopulation persistence. In contrast, the more localized scales for *O. swinhoana* (150–500 m stream order overlap) indicate a reliance on immediate riparian zones for core movements, consistent with its sedentary ecology and homing behavior. Moreover, the additional signal at 500 m in the roadkill models for this species suggests that excursions beyond core riparian zones are associated with increased road exposure and elevated mortality risk within the specific catchment and landscape context examined in this study. Collectively, these results indicate that stream order captures the spatial framework along which amphibian movements are organized, while tree cover, microclimate, and bioclimatic conditions modulate how species use this framework. For both species, stream order reflects access to breeding habitats and movement pathways, whereas tree cover and vegetation vigor contribute to moisture retention, shelter, and reduced desiccation risk during terrestrial movements. Species-specific responses to temperature, precipitation, and wind exposure further reflect differences in activity timing, breeding behavior, and movement tendency, explaining why identical structural features translate into different distribution and mortality patterns across species. Amphibian connectivity therefore emerges from the integration of multiple movement processes, including directional adult movements to breeding sites and more diffuse juvenile dispersal into surrounding terrestrial habitats, which together shape how individuals use stream–riparian landscapes. Variation in movement behavior among species, and even among individuals, means that identical structural features may support connectivity differently depending on species ecology and movement tendencies. These results support our hypothesis that stream order, when evaluated across multiple spatial scales, is associated with both amphibian occurrence and roadkill distributions, reflecting stream-network connectivity.

Bioclimatic predictors had relatively low to moderate importance (PI = 4.4–23.6%) but highlighted species key ecological traits. Both species identified precipitation as a significant factor in their occurrence and roadkill models, reflecting anurans' dependence on moisture due to their permeable skin, which makes their bodies sensitive to water loss (Kam and Chen 2000; Huang et al. 2004). However, species-specific differences were still evident. For *R. sauteri*, precipitation was the only bioclimatic predictor selected across both models, consistent with rainfall-driven breeding activity in anurans (Huang et al. 2004). This species, for instance, clusters in streams, grasses, and shrubs near shores after heavy or torrential rains (IUCN 2020b). Moreover, breeding season shifts with altitude: fall at 300–1,100 m, summer at mid-elevations around 1,600 m, and spring above 2,000 m (Lai et al. 2003). These microclimatic differences likely explain why different precipitation variables were selected (BIO14: driest month for occurrence; BIO18: warmest quarter for roadkill).

In contrast, *O. swinhoana* responded to both temperature and precipitation, with temperature playing the more critical role. Occurrence was influenced by annual mean temperature (BIO1), indicating sensitivity to general temperature conditions, together with precipitation during the wettest quarter (BIO16). However, the strongest effects were associated with roadkill, where the mean temperature and precipitation of the wettest quarter (BIO8, BIO16) were both

influential, with temperature almost twice as important (PI = 23.6 vs. 13.8). This aligns with the species' ecology, as its seasonal activity is primarily temperature-driven, while rainfall modulates breeding timing by influencing stream flow rates (Kam and Chen 2000; Lai et al. 2005). Physiological requirements explain this pattern, since metamorphosis, for instance, requires approximately two months, between November and April, depending on stream thermal conditions (Kam and Chen 2000). Seasonal records confirm this dual dependence on temperature and rainfall, with higher abundance in summer than in winter (Kam and Chen 2000; Lai et al. 2005), consistent with regional climatic patterns of wetter summers and drier winters (Chen et al. 2019).

Vegetation indices and topography contributed secondarily. NDRE–March, a proxy for canopy chlorophyll and vegetation health (Wavrek et al. 2023), was selected for both species' occurrence models, highlighting early-season riparian vegetation vigor as a driver of habitat suitability. Dense, photosynthetically active vegetation, combined with rising March temperatures, may stimulate frog activity after the cold, dry winter in northern Taiwan (Huang et al. 2001; Chen et al. 2019). The stronger effect for *O. swinhoana* (PI = 17.0) aligns with its preference for shaded forest creeks (IUCN 2020a). That both species selected NDRE–March indicates that this index complements stream order and tree cover by capturing vegetation quality, underscoring the importance of riparian buffers.

Unlike *R. sauteri*, which showed no sensitivity to wind exposure, *O. swinhoana* identified WEI as important in both occurrence and roadkill models, with negative responses in both cases (Suppl. material 1: fig. S3) and a slightly stronger effect in occurrence (PI = 5.9 vs. 4.7). This likely reflects the species' ecology: it is a sedentary, homing species that occupies hillside streams in broadleaf forests (IUCN 2020a). Although the species appears able to tolerate extreme wind conditions, as populations increased after a typhoon event (Kam et al. 1998), roadkill was associated with low-WEI valley-bottom sites, consistent with breeding in small, shaded mountain creeks (IUCN 2020a), which are typically more sheltered, where increased movements during the breeding season elevate road-crossing risk (Kam et al. 1998; Pittman et al. 2014; Arntzen et al. 2017; Churko et al. 2020). From a planning perspective, prioritizing mitigation in low-WEI valley corridors, where roads intersect amphibian habitats, can maximize conservation effectiveness. Overall, vegetation vigor and microclimatic conditions (WEI) refine habitat suitability and mortality risk within conflict zones, demonstrating that integrating fine-scale environmental variables such as WEI into connectivity assessments enhances the precision of mitigation planning.

Occurrence and roadkill suitability patterns

For both species, predicted occurrence suitability extended more broadly and into higher elevations than roadkill suitability, which was concentrated mainly at mid-altitudes (Figs 2, 3), likely reflecting their association with developed areas. This pattern likely reflects an overlap between persistent amphibian populations and sufficient traffic intensity at mid-elevations to generate road mortality, contrasting with highly urbanized low elevations where populations are often reduced and higher elevations where traffic levels are too low to produce substantial roadkill. A similar influence of altitude on amphibian roadkill patterns has been reported in Portugal, where roadkill decreased at higher elevations due

to reduced human activity and traffic intensity (Matos et al. 2012). Additionally, both occurrence and roadkill suitability closely followed the stream network, particularly evident in binary maps showing suitable areas aligning with stream corridors and extending into adjacent terrestrial habitats. In practical terms, this indicates that amphibian movements are concentrated along stream–riparian corridors and their immediate surroundings, increasing the likelihood of road crossings and mortality where roads intersect these pathways. Between species, *R. sauteri* exhibited patchier suitability patterns, whereas *O. swinhoana* showed a broader and more continuous spatial distribution for both occurrence and roadkill, particularly concentrated in recessed stream valleys, which are typically more sheltered. This pattern in *O. swinhoana* reflects its wide distribution and preference for humid, shaded environments, consistent with its ecology described earlier (Kam et al. 1998; Kam and Chen 2000; IUCN 2020a). The pronounced concentration of *O. swinhoana* roadkill at mid-altitudes and in valley-bottom habitats (Fig. 3) indicates that the species is particularly vulnerable where sheltered stream valleys coincide with these elevational zones. Valley bottoms provide stable hydrological conditions (Tonkin et al. 2018), cooler and more humid microclimates, and dense vegetation cover (Olson et al. 2007; Graziano et al. 2022), making them favorable for amphibian persistence but also increasing the likelihood of mortality hotspots when intersect with roads (van der Ree et al. 2015). Collectively, these findings indicate that topography and hydrology, together with vegetation structure, jointly shape amphibian connectivity and road-mortality risk, emphasizing the need to incorporate these factors into landscape-scale conservation planning and roadkill-mitigation strategies.

The strong association between amphibian distributions and stream order mirrors patterns observed in other aquatic groups (e.g., insects, fish, birds, mammals), where stream order and a site's position in the network shape species dispersal and persistence (Tonkin et al. 2018; Kuemmerlen et al. 2019; Graziano et al. 2022). Our results highlight stream–riparian connectivity as a key principle across aquatic–terrestrial systems. This enhances the generalizability of our findings and suggests that maintaining riparian buffer connectivity can simultaneously benefit multiple taxa.

Future pressures from climate change are expected to alter stream flow regimes and forest cover, with direct consequences for amphibian persistence (Haddad et al. 2015; Graziano et al. 2022). Shifts in precipitation may intensify seasonal breeding bottlenecks, while rising temperatures could expand elevational ranges of our focal species and other taxa (Maron et al. 2015). Integrating climate projections into models such as ours can guide connectivity adjustments and help ensure conservation effectiveness under changing conditions (Tonkin et al. 2018; Kuemmerlen et al. 2019).

Model evaluation and validation

Model evaluation metrics indicated consistently strong predictive performance (AUC = 0.794–0.933; CBI = 0.742–0.968), with low |AUC.diff| values (0.018–0.057). These results indicate limited overfitting and stable predictive capacity, enhancing the ecological reliability of our predictions (Radosavljevic and Anderson 2014). Although the roadkill models of *R. sauteri* showed the highest |AUC.diff| (0.057), suggesting reduced generalizability compared to occurrence

models, their predictions remained reliable (Radosavljevic and Anderson 2014). CBI values were consistently positive, ranging from moderate to very high, with occurrence models performing strongest (0.828–0.968). Roadkill models had lower values (0.742–0.763) but still provided informative predictions. Importantly, null-model tests confirmed that the |AUC.diff| values were significantly lower than random expectations, while AUC and CBI were significantly higher, reinforcing confidence in the ecological signal of our predictions (Wheatcroft 2020) (Table 2; Suppl. material 1: fig. S4).

A key methodological aspect of our study is the use of cross-dataset validation, which evaluates the ability of models trained on one ecological process (distribution vs. mortality) to predict patterns of the other. This provides a complementary test of transferability and a perspective beyond internal cross-validation. However, it does not represent fully independent validation in the strictest sense, since both datasets originate from the same monitoring framework (Fourcade et al. 2018). Cross-dataset results indicated that occurrence-based models validated successfully with roadkill records for *R. sauteri* and *O. swinhoana* (AUC = 0.884–0.918; CBI = 0.877–0.957). In contrast, roadkill-trained models performed less strongly when evaluated against occurrence records (AUC = 0.679–0.810), although CBI remained high (0.902–0.909), confirming reliable calibration despite weaker discrimination. Additionally, while AUC consistently exceeded null expectations, CBI significance appeared only for the *R. sauteri* occurrence model validated with roadkill data (Table 1; Suppl. material 1: fig. S5). This outcome is reasonable, as broader occurrence patterns can more reliably identify narrower, localized movement-risk patterns that do not generalize across the full distribution. Together, these results demonstrate that integrating both model types provides complementary insights into amphibian vulnerability. Nevertheless, the generalizability of these findings remains context dependent, and future studies incorporating independent catchments or regions will be critical to evaluate transferability, particularly where landscape structure, traffic intensity, or climatic conditions differ (Tuanmu et al. 2011; Fourcade et al. 2018). While MaxEnt can perform well with limited sample sizes when appropriately parameterized, PI values for the *R. sauteri* roadkill model (n = 11) should be interpreted with caution. In small datasets, PI can be sensitive to sample size, predictor collinearity, and model configuration. Accordingly, PI values here are best viewed as indicative of the relative ranking of variable influence within this case-study context rather than as absolute measures of ecological importance.

Although model evaluation and cross-dataset validation confirmed strong predictive and ecological performance, several limitations should be considered when interpreting these results. These include the absence of direct movement data, meaning connectivity was inferred from distributional proxies rather than observed movements. While multiscale buffers provide useful insights, buffer radius does not represent actual movement distance, so our approach is better interpreted as a connectivity analysis designed to support impact assessments for development rather than a direct movement study (Cumming and Tavares 2022; Karlsson and Bodin 2022; Kor et al. 2022; Paemelaere et al. 2023). Models also did not include anthropogenic variables such as traffic volume or land use (Fischer and Lindenmayer 2007), and the focus on two amphibian species limits generalization. Broadening the framework to

include human-related drivers and taxa with different ecologies (e.g., amphibians, birds, and mammals) would strengthen inference and extend stream connectivity as a cross-taxa conservation principle.

Stream connectivity implications for conservation and landscape design

Our results underscore the central role of riparian corridors, tree cover, and wind-sheltered valley bottoms in shaping amphibian occurrence and mortality risk. Different buffer widths and spatial scales translate into varying levels of connectivity and associated roadkill. Because these predictors reflect species-specific movement behavior, breeding ecology, and sensitivity to microclimatic conditions, effective conservation planning must align buffer design and mitigation measures with the ecological requirements of target species rather than applying uniform solutions. Based on our findings, riparian corridors and surrounding tree-cover patches emerged as indicative planning benchmarks within this catchment. Stream-order buffers of up to 750 m and tree-cover patches of up to 2000 m were associated with stronger connectivity signals and are likely to provide more continuous and sheltered corridors that reduce resistance to movement, minimize edge effects, and lower the energetic cost of dispersal. These values should be interpreted as context-dependent reference scales rather than prescriptive or universally applicable thresholds. Conversely, narrow or interrupted buffers can concentrate movements into high-risk zones where roads intersect streams, transforming potential connectivity pathways into mortality traps. In such areas, habitat-connectivity measures should be implemented, including amphibian underpasses or culverts combined with drift fencing to guide individuals toward safe crossing points. These structural measures can be further supported by temporary management actions, such as seasonal road closures, reduced speed limits, or temporary warning signage during peak movement periods, to reduce collision risk where permanent infrastructure is not feasible (van der Ree et al. 2015). These targeted measures can be precisely located in areas where stream-network connectivity coincides with elevated mortality risk. Together, these interventions translate connectivity principles into practical, scale-sensitive planning and design actions that reduce mortality while maintaining landscape permeability. By explicitly considering these scale-dependent relationships, conservation planning can better translate structural features (stream networks, tree cover) into actionable outcomes, balancing movement facilitation with mortality reduction. These thresholds are not proposed as rigid regulations but as indications for planning and design use derived from a framework applied to one catchment, based on crowdsourced occurrence and roadkill datasets of *R. sauteri* and *O. swinhoana*. While their direct transfer to other landscapes or taxa should be made cautiously, they provide practical benchmarks for designing connectivity interventions in mixed-use catchments with strong elevational and climatic gradients. Because fixed-width riparian buffers are often debated (Olson et al. 2007; Graziano et al. 2022), flexible, variable-width buffers are recommended to target zones of high ecological or hydrological importance while permitting sustainable land use (Peterson et al. 2013; Jyväsjärvi et al. 2020).

Wind exposure emerged as an additional driver of mortality, with low-WEI valley bottoms coinciding with *O. swinhoana* habitats and roadkill hotspots, chan-

neling movements into sheltered riparian corridors. Integrating all identified drivers and planning considerations, effective mitigation should combine structural, behavioral, and landscape-based strategies across priority areas such as riparian corridors, tree-cover patches, and wind-sheltered zones. Structural and temporal mitigation measures, as outlined above, can directly reduce mortality at conflict zones of stream–road intersections and mitigate collision risks during peak activity periods (van der Ree et al. 2015). Vegetation management offers further flexibility: enhancing shelter in lower roadkill-risk riparian zones (e.g., by using shelterbelt planting) can reinforce stream–terrestrial connectivity while diverting movements away from wind-exposed, high-traffic areas (van der Ree et al. 2015; Silva et al. 2019). Together, these interventions strengthen stream-network connectivity, lower mortality risk, and provide co-benefits for other riparian-dependent taxa (Tonkin et al. 2018; Kuemmerlen et al. 2019; Graziano et al. 2022), increasing the effectiveness of conservation efforts.

Taken together, incorporating stream–riparian connectivity assessments into EIAs provides a proactive mechanism to align amphibian conservation with environmental planning and design, preventing ecological degradation while avoiding costly retrofits (Karlsson and Bodin 2022; Torres et al. 2022; Paemelaere et al. 2023). Because altered rainfall regimes and temperature patterns are expected to reshape amphibian habitats and movement corridors, including climate change projections is essential for ensuring long-term effectiveness (Li et al. 2013). Connectivity outcomes can be further strengthened if measures are integrated with green-blue infrastructure that combines ecological functions with socio-economic benefits and other ecosystem services (Keeley et al. 2019; Paemelaere et al. 2023). By embedding stream-network connectivity into EIAs, planners can design multifunctional riparian corridors that benefit not only amphibians but also a wide range of riparian-dependent taxa, enhancing biodiversity conservation across the catchment. Despite its limitations, our catchment-scale approach demonstrates how stream networks can inform environmental planning. Climate change adds urgency, as altered flow regimes and forest loss may shift amphibian distributions, underscoring the need for flexible, connectivity-based planning (Haddad et al. 2015; Tonkin et al. 2018; Kuemmerlen et al. 2019; Tyagi et al. 2024). Although focused on two amphibian species in northern Taiwan, the framework is transferable across species and applicable in other regions. Stream-centered conservation planning has been successfully applied in Europe, North America, and Asia (Cumming and Tavares 2022; Karlsson and Bodin 2022; Kor et al. 2022; Kim et al. 2024), maintaining amphibian-rich riparian forests under development pressure. Embedding stream connectivity into EIAs would operationalize global initiatives such as the Kunming–Montreal Global Biodiversity Framework and the UNEP-WCMC Connectivity Conservation Focal Initiative (WCMC n.d.), aligning local planning with international biodiversity targets and reinforcing the broader conservation value of our study. In summary, the contrasting responses of the two focal amphibian species demonstrate why stream networks should be explicitly incorporated into future landscape planning. Despite differences in movement behavior and habitat use, both species exhibited strong associations with stream-network structure across occurrence and roadkill models, indicating that stream order provides a robust spatial framework for identifying movement pathways and mortality-risk zones. This consistency suggests that stream networks can

serve as effective planning proxies for connectivity, even when species differ in dispersal tendencies, and supports their use as a transferable basis for connectivity-oriented sustainable planning and landscape design.

Conclusion

This study demonstrates that integrating stream order as a multiscale predictor within an amphibian species distribution modeling framework effectively captures stream network connectivity patterns across the study catchment, as reflected in both occurrence and roadkill models. The strong model performance and cross-dataset consistency confirm that critical scales of stream order can efficiently describe amphibian distributions and that occurrence and roadkill data jointly reveal distinct stream-network connectivity patterns. Among environmental variables, tree cover, temperature, precipitation, NDRE (March), and wind exposure (WEI) were also important, with tree cover dominating permutation importance across models. In contrast, stream order showed a stronger association with roadkill models and a clearer mechanistic link to connectivity, highlighting its role in capturing movement pathways and mortality risk. Importantly, these findings translate directly into spatially explicit indicators that can support sustainable landscape planning and design where direct movement data are unavailable.

For both focal species, *Rana sauteri* and *Odorrana swinhoana*, predicted occurrence and roadkill suitability followed the stream network, with suitable areas aligning along stream corridors throughout the catchment. Occurrence suitability extended more broadly and reached higher elevations, while roadkill suitability was concentrated mainly at mid-elevations, reflecting the spatial overlap between persistent amphibian populations and road traffic, in contrast to lower elevations with higher traffic but reduced populations and higher elevations where traffic pressure is low. *O. swinhoana* exhibited a wider elevational range in both occurrence and roadkill models, concentrated in sheltered stream valleys, consistent with its broad distribution and preference for humid, shaded habitats. These patterns reveal ecological insights linking habitat suitability and roadkill risk to species traits and environmental drivers. Together, they emphasize that topographic exposure and hydrological structure jointly modulate species-specific connectivity, with WEI emerging as a practical indicator for prioritizing mitigation and conservation zones.

We recommend implementing scale-dependent planning thresholds and variable-width riparian buffers aligned with the stream network, supplemented by drift-fenced underpasses and other targeted temporal measures to sustain cross-road connectivity, particularly at mid-elevation areas. Strategic vegetation management to enhance shelter within lower-risk riparian zones could attract animals away from exposed, high-risk sites and reinforce stream–terrestrial connectivity. Together, these strategies provide actionable guidance for sustainable planning and design, reducing amphibian mortality while maintaining landscape permeability for multiple taxa. By combining empirical occurrence and roadkill data with spatial stream-network predictors, this framework provides a practical and transferable approach for embedding connectivity analysis into Environmental Impact Assessments, advancing sustainable planning and design.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

During the preparation of this work the author Panagiotis I. Karanasios used ChatGPT, Grok, editGPT, DeepSeek, and Skywork in order to paraphrase and improve English writing. After using these tools, the author reviewed and edited the content as needed and take full responsibility for the content of the publication.

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Author contributions

Panagiotis I. Karanasios: Conceptualization, Investigation, Data curation, Methodology, Writing — original draft preparation, Writing — review and editing. Dirk S. Schmeller: Methodology, Writing — review and editing. Yu-Pin Lin: Conceptualization, Methodology, Writing — review and editing, Supervision.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplemenatry figures and tables

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